CHAPTER TWO

Species–area curves and the geometry of nature

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Introduction

It is widely appreciated that species distributions and biodiversity can be strongly related to environmental factors. Likewise, it is recognized that increasing environmental heterogeneity with area is one of the determinants of species–area relationships. However, few theoretical treatments of species–area relationships specifically address *how* biodiversity's increase with scale should be related to the geometry of the environment. I hypothesize that this geometry is the underlying reason for the triphasic species–area curve.

Gradient analysis

One of the oldest, strongest and least contentious generalizations in ecology is that the spatial distribution of species is due, at least in part, to variation in the environment. In particular, the abundance of a species tends to be a unimodal function of important environmental variables (Whittaker, 1975; ter Braak, 1987; Austin & Gaywood, 1994). Such functions are termed species response curves, and graphs of the response curves for all species in a region combined or *coenoclines* (Fig. 2.1) are in almost all ecological textbooks (for example, Begon, Harper & Townsend, 1996; Ricklefs, 2001) and have played important roles in the development of ecological theory (Whittaker, 1972; Shmida & Ellner, 1984; Tilman, 1988). The study of how species respond to gradients in the environment is known as gradient analysis (Whittaker, 1967; Austin, 1987; ter Braak & Prentice, 1988).

   The unimodal species response curve is a simple manifestation of a species having an optimum set of environmental conditions. As conditions deviate from the optimum, the species will occur in less abundance. Classic competition theory (for example, Giller, 1984) and its derivatives (for example, Tilman, 1988) dictates that interspecific competition may decrease the breadth of the species response curve – that is, the "realized niche" is less than the "fundamental niche". However, the utility of gradient analysis and the validity of unimodal response curves do not depend on role or strength of interspecific interactions.
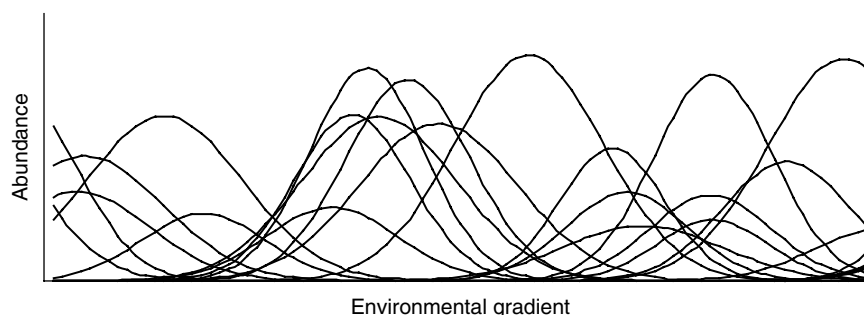
Figure 2.1 A hypothetical coenocline, consisting of the species response curves of all the species in a community. Although the curves illustrated here are mostly smooth and unimodal (one-peaked), the principles described here will hold with a modest amount of multimodality and noise in abundance.

An obvious consequence of the relationship between species and the environment is the *environmental heterogeneity hypothesis*: you expect to find more species in regions which are spatially variable in the environment (Palmer, 1992, 1994; Rosenzweig, 1995; Kerr & Packer, 1997; Burnett *et al.*, 1998; Fraser, 1998; Cowling & Lombard, 2002; Ewers *et al.*, 2005). This simple hypothesis has been verified in a number of systems (Kerr & Packer, 1997; Burnett *et al.*, 1998). Most environmental variables exhibit distance decay (Journel & Huijbregts, 1978; Burrough, 1981; Palmer, 1990; Bell *et al.*, 1993), meaning that heterogeneity in the environment increases as a function of spatial scale. Therefore, the species–area relationship should be largely determined by environmental heterogeneity (Williamson, 1988; Whittaker, 1998).

The geometry of heterogeneity and the species–area relationship

One of the biggest challenges in linking gradient analysis to the study of species–area relationships is that we have no comprehensive theory governing the geometry of environmental variation. Some environmental gradients vary smoothly and linearly: for example, the zonation of vegetation on a lakeshore (Nilsson & Wilson, 1991; Grace & Wetzel, 1998). Other gradients may be more spatially unpredictable, such as the distribution of light patches in an old-growth forest with numerous treefall gaps (Poulson & Platt, 1989; Hubbell *et al.*, 1999). Still other gradients, such as soil nutrients (Palmer, 1990) may have an intermediate degree of spatial predictability.

Furthermore, the geometry of environmental heterogeneity can change as a function of scale. While the edge of a lake has a well-defined slope, the distributions of lakes within a county may be not as easy to describe with a few parameters. On a yet broader scale, the frequency of lakes in a continent may be

a predictable function of climate. Thus, the component of the species–area curve that is caused by environmental heterogeneity is likely to behave differently at different scales.

The fractal geometry of the landscape and species richness

Fortunately, the science of Fractal Geometry (Mandelbrot, 1983) allows us to quantify and model the geometry of environmental heterogeneity (Burrough, 1983; Milne, 1992). This is most clearly illustrated by taking a line transect through a landscape (Fig. 2.2). The value of an environmental variable (or "regionalized variable" in the sense of geostatistics) as a function of a linear transect is topologically a line (a 1-dimensional object) embedded within a 2-dimensional space (defined by one spatial axis and one environmental axis). In this case, the environment's fractal dimension (D) ranges from 1 to 2. If the environment behaves as a smooth function of position along a transect, the function is very close to a line, and therefore has a D close to 1. If the environment is spatially unpredictable, the graph of environment as a function of position practically fills the plane. As a plane is a 2-dimensional object, D is close to 2. Most environmental variables will have an intermediate degree of predictability, and hence the fractal (or fractional) dimension will be somewhere between 1 and 2.

If we consider a 2-dimensional landscape (not just a line transect through it), a regionalized variable will be topologically 2-dimensional, but embedded in a 3-dimensional space. Its fractal dimension will therefore vary between 2 and 3. This is analogous to a smooth piece of paper being essentially a 2-dimensional object, but a highly crinkled piece of paper will be close to 3-dimensional. If the regionalized variable under consideration is elevation, then all dimensions are spatial.

There is an ample literature providing formal definitions of fractals, fractality, multifractals, self-similarity, self-affinity, and related concepts. Such precise concepts are important for simulations and theoretical treatments of fractals (see Šizling & Storch; Lennon *et al.*; Borda-de-Água *et al.*; and He & Condit, this volume). However, the use of fractal dimensions to get an empirical handle on the geometry of nature does not depend on such precise definitions. Most theoretical treatments of fractals involve a self-referent function (Feder, 1988): that is, a mechanism that generates self-similarity. It may be impossible to identify such functions in a complex natural setting; indeed they may not exist. But this is not an impediment for the use of fractal language to describe irregularity in nature.

The accumulation of new environments, and hence new species, as a function of area will differ depending on the fractal dimension. For example, one does not need to traverse a great distance to encounter numerous habitats in a high D
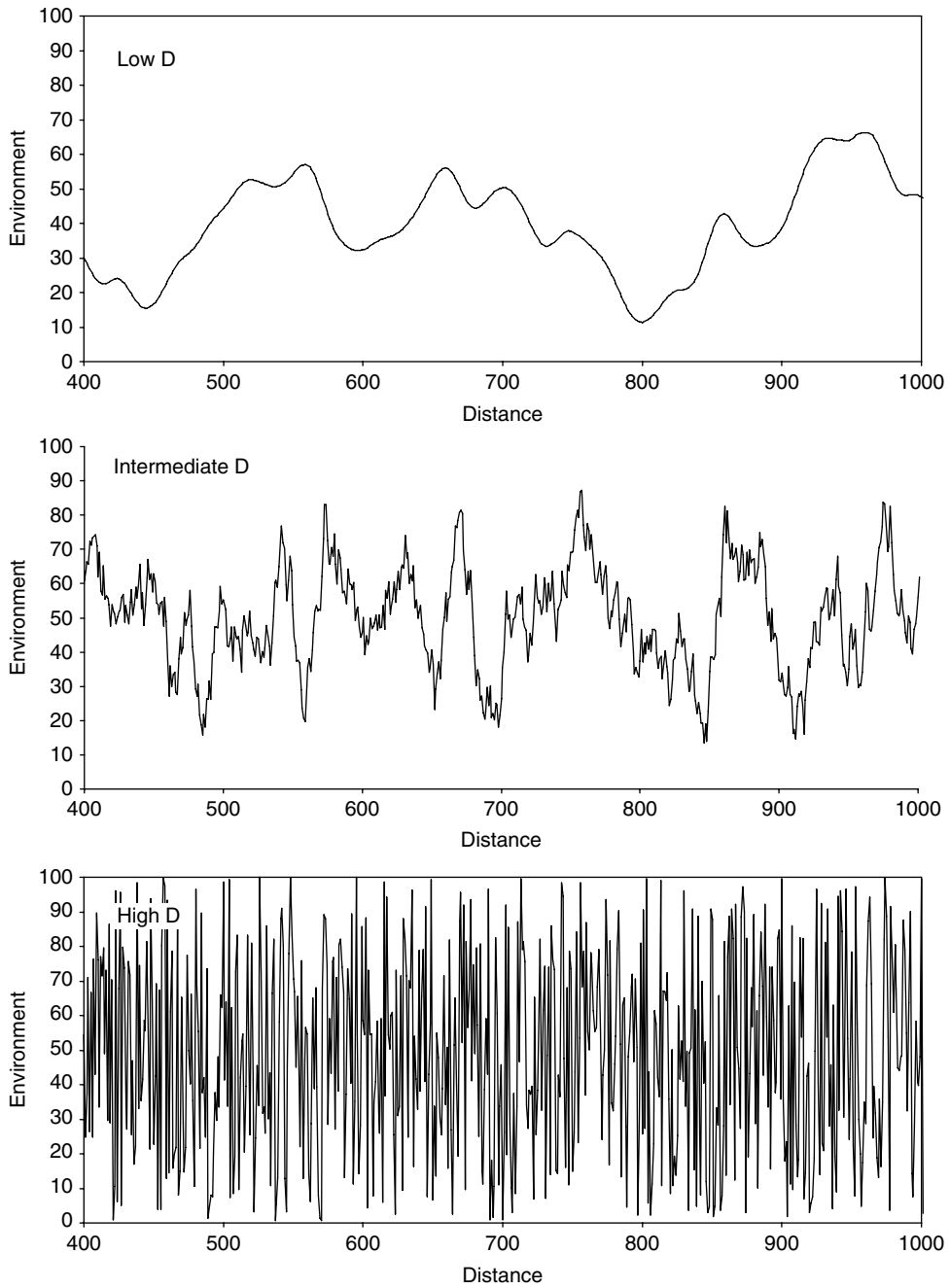
Figure 2.2 Three hypothetical examples of environmental heterogeneity along transects, ranging from smoothly varying (low fractal dimension) to white noise (high fractal dimension).
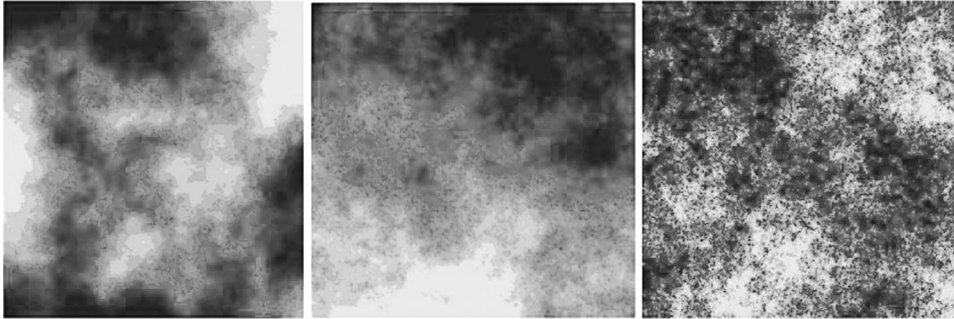
Figure 2.3 Simulated landscapes of 256×256 cells, in which the value of an environmental gradient varies from 0 to 100, as indicated by darkness. From left to right, the landscapes have fractal dimensions of 2.1, 2.5, and 2.9 and were constructed with the midpoint displacement algorithm (Saupe, 1988).
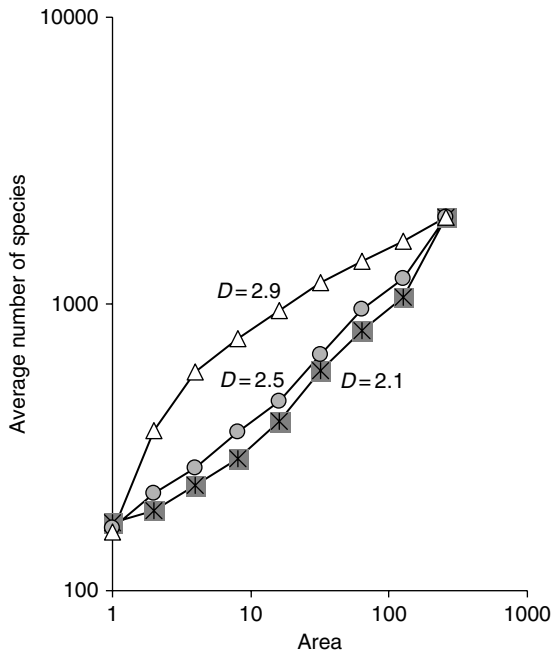

Figure 2.4 Species–area curves (each point is the average of 10 simulated square quadrats) for landscapes differing in fractal dimension (Fig. 2.3). The environment of each landscape varied between 0 and 100, and each of 2000 species occurred in the landscape wherever the environment was suitable. Each species had a habitat breadth of 10 units, and the midpoint of each species' range was randomly chosen between -5 and 105. The midpoints can fall outside the range of the environment, much as the species optimum may fall outside the environmental conditions in real landscapes (see Fig. 2.1).

environment, in contrast to a low D environment (Fig. 2.2). I illustrate this further by simulating 2-dimensional landscapes (Fig. 2.3). The landscape with the highest D initially accumulates species at the fastest rate, as most environments are sampled at the finest scales (Fig. 2.4). Note that landscape geometry influences not only the location (that is, left to right and up to down position) but also the shape of the species–area relationship.

It is worth noting that the fractal dimension is only one descriptor of environmental texture. Landscapes (real or simulated) with the same D can be generated

in different ways. For example, one can generate smoothly varying low-D landscapes by averaging out random variation (as in Fig. 2.2) or by assigning linear or curvilinear functions of space (as in Fig. 2.3). However, the effects of such on species richness patterns are not likely to be dramatic.

Multiple gradients

Species composition responds to multiple environmental factors, not just one. Indeed, modern gradient analysis can be viewed as an act of *dimension reduction* (Gauch, 1982; Lepš & Šmilauer, 2003). Although the potential number of gradients is practically limitless, there tend to be relatively few important factors determining species composition (Gauch, 1982; Whittaker, 1975). The existence of even two or three factors greatly complicates the relationship between heterogeneity and scale. For example, different variables may have different underlying fractal dimensions.

To illustrate this principle, I simulated two 100×100 cell landscapes, each with two important gradients (ranging from 0 to 100). I arbitrarily defined three spatial scales: a fine scale consisting of the individual cell, an intermediate scale consisting of a 10×10 cell block, and a broad scale consisting of the entire landscape. For both landscapes, gradient 1 was complex (high D) at an intermediate scale: each block of 10×10 cells was assigned a uniform random value between 0 and 100. Landscape A had fine-scale linear pattern for gradient 2: it varied between 0 and 100 as a linear (low D) function of easting and northing within each 10×10 cell block. The direction of increase (east, west, north or south) was randomly chosen. Landscape B had a broad-scale linear (low D) pattern for the gradient 2: it increased from 0 to 100 from south to north (as there is no net directionality to the rest of the simulation, the choice of direction is inconsequential).

I randomly located the midpoints of each of 1500 species along each gradient in each landscape. Each species had a habitat breadth of 10 units along both gradients. A species would only occur in a cell if both factors were simultaneously within the appropriate range. I then sampled each landscape using 10 replicates of each of 11 spatial scales, ranging from 2 cells on a side to 90 cells on a side, and counted the species in each.

Figure 2.5 illustrates that landscapes A and B have dramatically different species–area curves. Each curve has an inflection. Landscape A has a steep initial slope associated with the fine-scale, low-D gradient. Once several of the 10×10 cell blocks have been encountered, most of the environmental variation has been sampled, and the curve levels off. In contrast, landscape B has a low initial slope within the blocks, because neither gradient varies appreciably at that scale. The slope does not decrease at broad scales because of the broad-scale, low-D gradient. In other words, an increase in grain (above the scale of the block) invariably leads to sampling new environments.
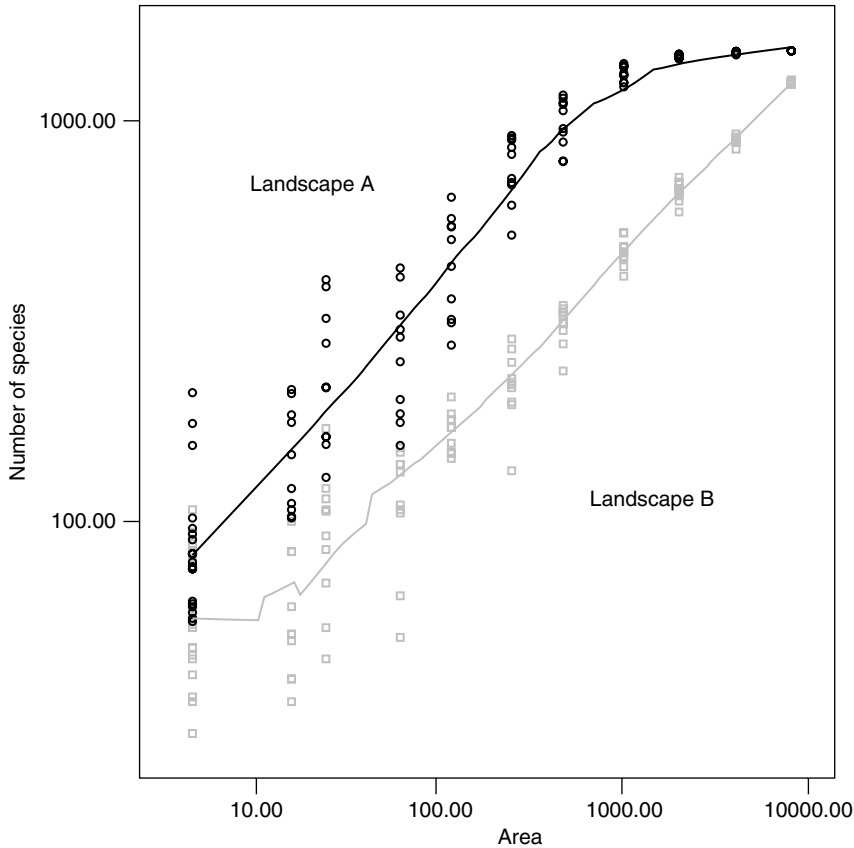
Figure 2.5 Species–area curves for two hypothetical landscapes, as described in the text. Both landscapes have one gradient with a high D at an intermediate scale. Landscape A has a secondary gradient that has a high fractal dimension at a broad scale, and a low fractal dimension at the fine scale. Landscape B has a secondary gradient with a low fractal dimension on a broad scale. Curves are LOWESS fits.

At intermediate spatial scales, the two species–area curves are parallel. This is undoubtedly due to the fact that gradient 1 is identical between the two landscapes.

I have shown two simple but arbitrary configurations for a two-gradient system. The bewildering variety of *possible* combinations of variables, scales, and geometries might doom any synthetic theory of species–area curves in heterogeneous landscapes (that is, all real landscapes). However, I will argue below that there may be general principles underlying the geometry of the environment, and these could lead to a fuller understanding of the species–area relationship.

The Environmental Texture Model of the triphasic species–area curve

When viewed over many orders of magnitude of grain, species–area curves tend to be triphasic: they are steep at fine and broad scales and shallow at intermediate scales (Shmida & Wilson, 1985; Rosenzweig, 1995; Hubbell, 2001;

Williamson, Gaston & Lonsdale, 2001). The near-universality of such curves strongly implies that they have a general explanation. Thus, the triphasic relationship has spurred widespread interest for ecological theory. Two of the boldest theoretical treatments of the triphasic curve (Rosenzweig, 1995; Hubbell, 2001) invoke fine-scale random sampling and broad-scale dispersal limitation as the main determinants of the relationship; they do not fully integrate environmental heterogeneity into theory.

Given that the geometry of the environment has a great potential to influence the shape of species–area relationships (Figs. 2.3–2.5), it is worth asking whether it could be the root cause of the triphasic pattern. Here, I propose that the environment tends to have a low fractal dimension at fine scales and broad scales, and a high fractal dimension at intermediate scales. Because the geometry or "texture" of the environment varies as a function of scale, I term this the *Environmental Texture Model of the triphasic species–area curve*.

The previously described simulations, for convenience, assumed that gradients were all equally important, all species had similar responses to the environment, and there was no qualitative noise. Violating such assumptions would undoubtedly have effects on the shapes of species–area relationships. However, I must stress that the Environmental Texture Model has no such assumption: it merely stresses that the rate at which species accumulate as a function of scale will be influenced by the rate at which new environments appear, which in turn will be regulated by the underlying geometry of multiple environmental gradients.

In the following discussion, the definitions of fine, intermediate, and broad scales are admittedly arbitrary. As discussed later, these scales are likely to vary between regions. However, to frame the discussion, I consider "fine" scales to typically be less than a hectare, and "broad" scales to be greater than a million hectares.

Low *D* at fine scales

At fine scales, spatial variation in the environment is often dominated by topography (Wondzell, Cornelius & Cunningham, 1990; Norton, 1994; Umbanhowar, 1995; Clark, Palmer & Clark, 1999; He, LaFrankie & Song, 2002). Gravity, along with flaking of rock and other erosional processes, tends to decrease roughness or fine-scale complexity in the environment. Indeed, we often take the topographic smoothness of the landscape for granted – the rough, irregular, or complex elements of landscapes are often considered points of special beauty or interest, and occupy a relatively tiny portion of the landscape.

Gravity also tends to even out the water table on a fine scale – so hydrological influences on species composition (Wassen & Barendregt, 1992; Zunzunegui, Diaz Barradas & Garcia Novo, 1998) also tend to have low fractal dimensions.

Variation in soils can influence fine-scale distribution of plant species (Cox & Larson, 1993; Oliveira-Filho *et al.*, 1994; Tuomisto *et al.*, 2002). Substantial fine-scale

variation can exist in soils, and have a high fractal dimension (Palmer, 1990). However, rhizospheres are able to integrate over such fine-scale variation (Schmid & Bazzaz, 1987; Evans & Whitney, 1992; Wijesinghe & Hutchings, 1997). Similarly, the mass effect (Shmida & Ellner, 1984; Auerbach & Shmida, 1987; Palmer, 1992; Bengtsson, Fagerström & Rydin, 1994; Onipchenko & Pokarzhevskaya, 1994) or "vicinism" (van der Maarel, 1995; Zonneveld, 1995) will tend to make the *effective* environmental heterogeneity smoother than the *actual* environmental heterogeneity. Not being rooted, most animals will also be able to average out fine-scale variation in the environment.

High *D* at intermediate scales

Imagine a soil map or a vegetation map for a state, province, or small country. More often than not, the soil types or vegetation types (admittedly arbitrary categories) exist as small, often complexly shaped patches scattered throughout the landscape. Perhaps as a root cause of this, topography at such scales often has a high fractal dimension. As scale is increased, the topographic variation that is smooth on the scale of a hill or a valley gives way to the complex (high *D*) variation of multiple hills and valleys.

It is worth noting that as *D* approaches 3, the landscape can be considered *homogeneous* (*sensu* Palmer, 1988; and Šizling & Storch, 2004). Homogeneity does not refer to within-landscape variation, but rather the fact that the landscape remains similar upon subdivision. It is unlikely that there are scales at which any landscape is truly homogeneous, but it is quite likely that most landscapes exhibit more homogeneity at some scales than at other scales.

It might seem inappropriate to mention anthropogenic patterns in a discussion of triphasic curves. However, there are few large regions untouched by human activities. Given that humans have a profound effect on the geometry of the environment, it would be folly to ignore anthropogenic patterns. It is often said that humans tend to homogenize the landscape. This may be true at the scale of individual fields or other pieces of managed land. When we consider a small number of adjacent pieces of managed land, we have a low *D*: there are predictable, uncomplicated spatial trends. However, at the scale of multiple management units (for example, agricultural fields, forest stands) anthropogenic effects may be "patchy" and hence have indeed a high *D*.

Low *D* at broad scales

The spherical shape of the Earth causes differential heating of its surface. This simple fact, along with the Earth's rotation and tilt, is responsible for smoothly varying patterns of climate (for example, temperature, rainfall). The fact that air and water are fluids, and therefore are well mixed relative to solids, causes fine-scale and intermediate-scale spatial variation (that is, "weather") to be relatively short-lived or smooth. The relationship between climate and species composition is strong

(Retuerto & Carballeira, 1991; Hallgren, Palmer & Milberg, 1999; Qian *et al.*, 2003; Currie, this volume), and has been appreciated for a long time (von Humboldt & Bonpland, 1807). Because climatic variation has a low D, increasing the grain will always increase environmental heterogeneity at broad scales.

Exceptions

The argument that D is likely to vary with scale as described above is likely to be less than convincing. There are numerous obvious exceptions. For example, karst topography (a highly dissected geomorphology caused by the dissolution of limestone) illustrates high D at fine scales. Similarly, there are counterexamples to "high D at intermediate scales". Coastal plain regions may have a broad, smooth spatial gradient related to sedimentation history and groundwater hydrology. Mountains can cause high-D spatial variation in climate at relatively fine scales due to adiabatic processes and the rain shadow effect.

The existence of such exceptions gives us the ability to test the Environmental Texture Model. For example, we might expect a coastal plain to lack a well-defined triphasic curve, as increasing area at an intermediate scale will accumulate new environments at a rapid rate. Even if the basic model (low D–high D–low D) is correct, we should expect the shape of the triphasic to vary among regions. The first inflection point for a region with short inter-ridge distances, for example, should be to the left of that for a region with long inter-ridge distances.

The case of mountainous regions

Mountains represent a particularly interesting but complex challenge to the Environmental Texture Model (Fig. 2.6). The effects of gravity are the same as in nonmountainous regions. Thus, at fine scales, mountains should have low D at fine scales (though for various reasons, especially in regions with active
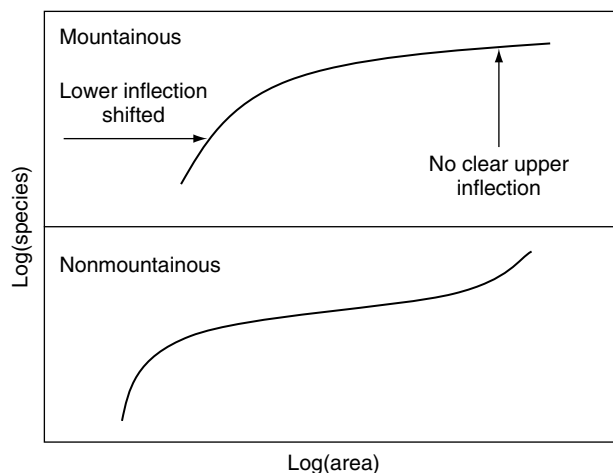

Figure 2.6 Hypothetical species–area curves for mountainous and nonmountainous regions, as discussed in the text.

orogenesis, I expect fine-scale D to be slightly larger than in nonmountainous regions). However, by definition, mountains are tall. Given the effects of gravity, they will also tend to be broad (with exceptions of some mesas). Therefore, the scale at which low D gives way to high D will be greater in mountainous regions. A high D occurs when multiple mountains or ranges are sampled; adding yet another mountain does not add much to environmental heterogeneity (unless bedrock or other characteristics differ). On a broad scale, we are unlikely to see an upward inflection. This is because the broad-scale (low D) climatic gradients are masked by the finer-scale orogenic climatic effects. In other words, a wide range of climates have already been sampled.

Richness of North American vascular floras in mountainous regions

In order to investigate the potential effect of mountainous regions on species–area relationships, I utilized data from The Floras of North America Project (http:// botany.okstate.edu/floras; Palmer, Wade & Neal, 1995; Withers *et al.*, 1998; Palmer *et al.*, 2002; Palmer 2005), which is an attempt to collect all vascular floras (plant species lists) written within North America north of Mexico. To date, my colleagues and I have gathered approximately 8000 references. While about 3000 of these contain valid data (Fig. 2.7), we have only extracted useful information
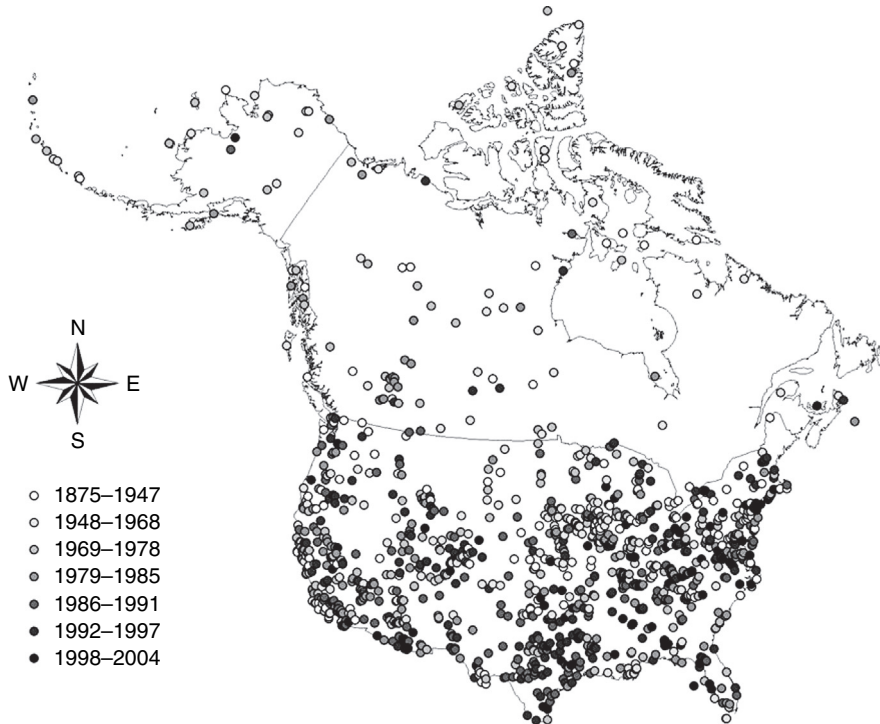

Figure 2.7 Locations of centroids of vascular floras in the Floras of North America Project, with markers indicating year of study.
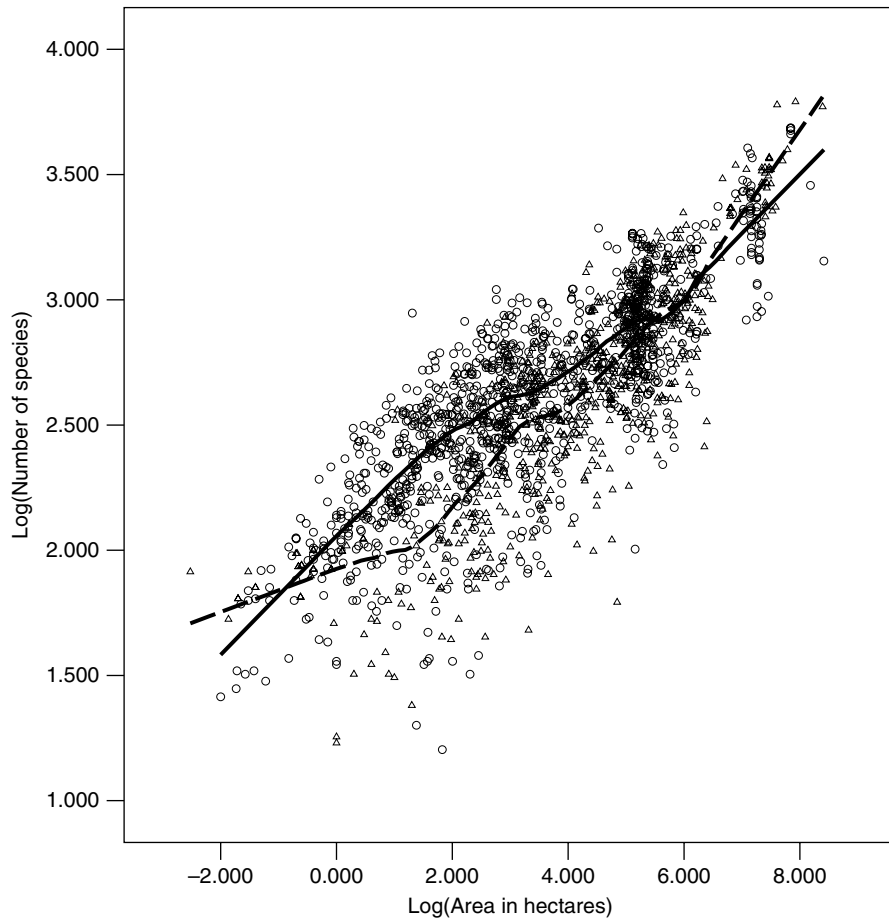
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Figure 2.8 Species–area curves for floras from mountainous regions (triangles and dashed line) and nonmountainous regions (circles and solid line). Lines are LOWESS curves.

from about 2200 floras. For this study, I restrict analysis to the 1815 floras south of 49° latitude and published after 1910. I then subdivided the continent (rather arbitrarily) into mountainous and nonmountainous regions.

Figure 2.8 demonstrates that mountainous and nonmountainous regions have quite different species–area curves. However, the difference is quite unlike the predicted difference (Fig. 2.6). The curve for nonmountainous regions is arguably (but not convincingly) triphasic. In mountainous regions, the initial slow increase at scales less than 10 ha gives way to a more rapid increase without any leveling off at broad scales.

My interpretation of this pattern is that alpine systems are fairly rich at fine scales, because of small individual size. This is coupled with a sampling bias, because botanists studying mountainous regions are more interested in the

higher elevations (thus the lowlands will not be sampled with small floras). However, at scales of one to thousands of hectares, there is a steep increase due to the low D nature of the elevation gradient. The mountain curve lies below the other curve at most scales, because of the altitudinal diversity gradient (Odland & Birks, 1999; Grytnes & Vetaas, 2002). The curve remains steep beyond the scale of individual mountains, either because different ranges are truly environmentally different, or because mountainous landscapes are likely to contain high numbers of local endemics. At broad scales, the number of species in mountainous regions surpasses that of nonmountainous regions because of enhanced environmental heterogeneity.

I cannot predict whether the rank speculation of the previous paragraph, or even the empirical patterns themselves, will stand up to more careful evaluation. The data have tremendous scatter that are caused by both methodological and biological factors. Furthermore, floristic data are known to have biases (Palmer, 1995; Palmer *et al.*, 2002). A set of many carefully chosen, nested species–area curves over many orders of magnitude of scale are likely to be of more value than the shotgun approach of Fig. 2.8. Nevertheless, it is clear that the geometry of the environment, perhaps interacting with phylogeny and patterns of long-distance dispersal, plays a critical role in determining the shape of species–area relationships.

Conclusions

The theory that the geometry of the environment can strongly affect species–area relationships is a rather simple and perhaps obvious one. In fact, geometric explanations have been articulated before.

In most cases, increasing the area from 1 ha to 10 ha will add very few new species. At this scale, at least for vertebrates, habitats tend to be similar and easily reached by dispersing individuals. By contrast, increasing the area from one-tenth of the continent to the entire North American continent will result in the addition of many new species (Brown, 1995).

The pattern of environmental variation is to some extent fractal. This fact, and the variation in the fractal dimension, may, in time, lead to a deeper understanding of the causes of the variability of species–area curves (Williamson, 1988).

Williamson (1988) recognizes that the slope of the species–area relationship may be directly related to the fractal dimension or "reddened spectrum" of the environment. The Environmental Texture Model can thus be considered an extension of Williamson's thinking to multiple scales and multiple gradients.

It is possible that the reason geometric explanations have been largely ignored is because they are not very glamorous – or because their parameters are hard to assess. In particular, we need to discover which environmental variables are important, and at which scales. Another downside of a strong geometric signature is that it may obscure other interesting, and more

biological, phenomena (such as the "correlation length" of Hubbell, 2001; or the "interprovincial" curve of Rosenzweig, 1995). Indeed, the Environmental Texture Model practically ignores biology (beyond the assumption that species distributions are influenced by the environment); explanations lie in the realm of geomorphology, geology, and climatology.

The Environmental Texture Model complements studies of species of varying spatial distributions (such as Šizling & Storch, 2004; Šizling & Storch, this volume). The species–area relationship is a simple property of the geometry of species distributions *and their covariances*. The environment plays a strong, but not exclusive, role in structuring species distributions. Patterns of interspecific covariance may help distinguish between the environment and other factors influencing the species–area relationship (Wagner, 2003).

It is perhaps most useful to consider the geometric theory to be a null model. It is when biodiversity patterns are *not* simple reflections of the underlying environmental template that we are likely to uncover macroecological phenomena. There needs to be more detailed study of this environmental template, and more focus needs to be directed to nonbiological disciplines such as geomorphology. Distinguishing between the Environmental Texture Model and alternative models (such as those involving sampling effects and dispersal limitation) will prove exceptionally challenging. Or in the words of Williamson 1988, "the techniques needed are appreciably more difficult; the results should be correspondingly more interesting".

Acknowledgments

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